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The genus *Orionis* Shaw (Hymenoptera, Braconidae, Euphorinae) in the Old World

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Abstract
The euphorine braconid genus *Orionis* Shaw, 1987 is found to be more diverse in the Old World than had previously been recognised. *Orionis* was regarded previously as largely Neotropical, with one Oriental species (*Orionis orientalis* Shimbori & Shaw, 2016) known from Thailand, but we recognise an additional three species from the Oriental and Palaearctic regions. Three species of Euphorinae are transferred to *Orionis* Shaw, 1987 and are new combinations: *Orionis coxator* (Belokobylskij, 1995), **comb. nov.**, *Orionis erratus* (Chen & van Achterberg, 1997), **comb. nov.**, and *Orionis flavifacies* (Belokobylskij, 2000), **comb. nov.** Previously known from the Far Eastern Palaearctic, *O. coxator* has surprisingly been found in Europe, in Belgium, England and the Netherlands. The inclusion of these species in *Orionis*, whereas most previous species have been described from the Neotropics, is justified by Bayesian analysis of the D2 region of 28S, Cytochrome Oxidase I barcode sequences, and morphology.

Keywords
Bayesian, new record, parasitoid, phylogeny, taxonomy

Introduction

On 29th September 2020, GRB caught a braconid wasp (Hymenoptera: Braconidae) at an actinic light in his garden in South-east England (Fig. 1). It seemed to be either a species of *Meteorus* Haliday or *Perilitus* Nees but was atypical for either placement. Perplexed as to what this could be, and sure it was nothing he had seen before, GRB sent a

leg to JS for barcode sequencing. The resulting species identification was '*Perilitus*' *coxator* Belokobylskij, 1995, with high probability, but the implications were interesting, as this and other similar species described from China ('*Perilitus*' *erratus* (Chen & van Achterberg, 1997)) and Russia ('*Perilitus*' *flavifacies* Belokobylskij, 2000), are clearly atypical for *Perilitus*, which prompted us to re-evaluate the generic classification of these species.

Material and methods

Specimens and images

Institutional abbreviations:

NHMUK Natural History Museum, London, UK;
ZISP Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia;
NHRS Swedish Museum of Natural History, Stockholm, Sweden.

The English specimen (NHMUK014425411) was collected at a white sheet with a 15W actinic bulb. The right hind leg was removed from the dry, card-pointed specimen for sequencing. Photos were taken with a Canon SLR EOS 5DSR with either a 65 mm macro lens or a Mitutoyo 10 × lens in combination with a 70–130 mm macro lens, mounted on a copy stand with an automated Z-stepper; images were aligned using Helicon Focus software version 6.6.1.

Morphological terminology follows van Achterberg (1993).

DNA extraction and sequencing

DNA was extracted from the hind leg using the Thermo Labsystems KingFisher extraction robot at the NHRS laboratory facility. The standard DNA barcode fragment of the mitochondrial cytochrome oxidase I (CO1) gene was obtained using primers by Folmer et al. (1994). Ready-To-Go PCR beads were used (Amersham Pharmacia Biotech, Amersham, UK) on the following program: 5 min 94 °C hot- start; 40 cycles: denature 94 °C for 15 s, anneal 46 °C for 15 s, extend 72 °C for 15 s; final extension 72 °C for 10 min. This gene has been used in previous studies of braconid phylogenetics (Belshaw et al. 2000; Belshaw and Quicke 2002; Dowton et al. 2002; Zaldívar-Riverón et al. 2006; Sharanowski et al. 2011; Stigenberg and Ronquist 2011), but latterly mainly in combination with other, particular nuclear, genes. In addition to the CO1 gene we also utilised the nuclear 28S D2 fragment (see Stigenberg and Ronquist 2011). PCR products were purified with EXO1 and FastAP. The product was sequenced using both the forward and reverse primers. Sequences were assembled and edited using Geneious Pro v.9.1.8. The Voseq v.1.7.4 (Peña and Malm 2012) database was used for storing voucher and DNA sequence data. BLAST analysis was performed to identify similar sequences within the NCBI database.

Phylogeny reconstruction

Bayesian Inference analyses were performed using MrBayes 3.2.7a (Ronquist et al. 2012). All BI analyses were performed through the Cipres web portal for phylogenetic analysis (Miller et al. 2010) (http://www.phylo.org). The protein coding CO1 was partitioned after codon positions 1+2 and 3, the 28S dataset was not partitioned. The Bayesian analysis was performed by running four MCMC chains for 10 million generations, sampling post-burn-in trees every 1000 generations. A CO1 analysis including 60 taxa as well as a combined CO1+28S analysis including 65 taxa were run. The datasets included an assortment of members of the Euphorinae tribe Perilitini with an ichneumonid and distant as well as closer braconids as outgroups. GenBank accession numbers for the *Orionis* species are shown in Table 1.

Results

In all our BI analyses we recovered the genus *Orionis* as monophyletic with 100% support. The reverse strand of CO1 was not successfully amplified for the English specimen (Euph_220), but the forward strand (GenBank ID: MW401798) was of good quality and on a BLAST search matched with '*Perilitus*' *coxator* with 96.7% similarity. The specimen was compared with the original descriptions of *P. coxator* (Belokobylskij 1995) and the apparently similar *P. erratus* (Chen and van Achterberg 1997); Sergey Belokobylskij then kindly compared images of the English specimen with specimens of *P. coxator* in ZISP. Bayesian analyses of CO1 barcode sequences as well as combined CO1+28S analyses of Perilitini species, including the sequence generated for this study, resulted in a topology (Fig. 2; the full phylogenies are presented in Suppl. material 1, 2) largely congruent with that of Stigenberg et al. (2015), with a monophyletic *Orionis*, including '*Perilitus coxator*' and '*P.*' *flavifacies* Belokobylskij, 2000 alongside *O. eximius* (Muesebeck, 1955), the type species of *Orionis* (Shaw 1987), and *O. orientalis* Shimbori & Shaw, 2016. Based on morphological synapomorphies (see Discussion) and the results of the phylogenetic analyses, *Orionis coxator* (Belokobylskij, 1995) and *Orionis flavifacies* (Belokobyslkij, 2000) are both new combinations.

The original description (Chen and van Achterberg 1997), including very useful illustrations, clearly shows that *Meteorus erratus* shares the synapomorphies of *Orionis*, and *Orionis erratus* (Chen and van Achterberg, 1997) is a new combination.

Table 1. GenBank accession numbers for *Orionis* sequences.

Specimen	COI	28S	Country
JS10_00511 *P. coxator*	KJ591484	KJ591277	Russia
JS10_00526 *P. coxator*	MZ021572	KJ591278	Russia
Euph_220 *P. coxator*	MW401798	MW600657	UK
JS10_00510 *P. flavifacies*	KJ591486	KJ591279	Russia
AB097 *O. eximius*	KJ591480	KJ591272	Costa Rica
GB_orionis *O. eximius*	-	AJ302824	unknown
AB101 *Orionis orientalis*	-	KJ591273	Thailand

Building on Shaw (1987) and Bortoni et al. (2016), we propose that *Orionis* can be diagnosed by the following combination of character states: frons with rugose or strigose sculpture (Fig. 3c); eyes strongly convergent ventrally (Fig. 3a); first metasomal segment long and slender, lacking dorsope or laterope, curved in lateral view, with spiracles around or not far posterior to the mid-length (Fig. 3c); propodeum strongly convex, with distinct dorsal and posterior faces of about equal length and often clearly separated by distinct bend/angulation (Figs 1, 3c).

However, two or three of those characters can be found in combination in some *Perilitus* species and the separation of these two genera is not entirely clear-cut. The key to Old World *Orionis* species presented here is based largely on the literature, and additional species might be expected.

Key to Old World species of *Orionis*

1 Face yellow; propodeum with rounded division between dorsal and posterior faces **2**

– Face black; propodeum with division between dorsal and posterior faces almost a right angle **3**

2 Pronotum and propleuron yellow; first metasomal tergite dorsally weakly rugose [Thailand] .... ***O. orientalis* Shaw & Shimbori**

– Pronotum and propleuron black; first metasomal tergite dorsally entirely striate [Eastern Palaearctic] .... ***O. flavifacies* (Belokobylskij)**

3 Ovipositor sheath 1.4–1.6 × length of the first tergite; hind coxa dorsally with some curved striae [Palaearctic] .... ***O. coxator* (Belokobylskij)**

– Ovipositor sheath about 2.0 × length of the first tergite; hind coxa dorsally rugose-punctate [China and Korea]..... ***O. erratus* (Chen & van Achterberg)**

Old World species of *Orionis*

Bortoni et al. (2016) revised the species of *Orionis* known to them, which included four Neotropical species and one from Thailand. Including the species transferred here to *Orionis*, the genus is now represented by equal numbers of described species in the Old and New Worlds. None has a recorded host.

Taxonomy

Genus *Orionis* Shaw, 1987

Type species. *Perilitus eximius* Muesebeck, 1955 by original designation.

Orionis coxator (Belokobylskij, 1995), new comb.

Perilitus coxator Belokobylskij, 1995.

Comments. Described from Russia, Primorskiy Territory (Belokobylskij 1995), subsequently recorded from Korea (Ku et al. 2001). Russian (Primorskiy Territory) specimen sequenced by Stigenberg et al. (2015). The record of *'Perilitus erratus'* from the Netherlands (van Achterberg et al. 2020) probably refers to this species.

Diagnosis. Mostly black, head with dorsal reddish patches; propodeum with posterior and dorsal faces angled about 100° relative to each other; hind coxa dorsally with curved striae; first metasomal tergite weakly striate medially (Figs 1, 3).

Specimens examined. ENGLAND • 1♀; Kent, Tonbridge; 51.186N, 0.287E; 29th September 2020; actinic light; G.R. Broad; NHMUK014425411; new record for the United Kingdom.

Orionis erratus (Chen & van Achterberg, 1997), new comb.

Meteorus erratus Chen & van Achterberg, 1997
Perilitus erratus: Belokobylskij (2000b)

Comments. Described from Oriental and Palaearctic Provinces of China: Guizhou, Liaoning and Yunnan (Chen and van Achterberg 1997); recorded from Korea by Papp

Figure 1. Lateral habitus of *Orionis coxator* (NHMUK014425411). Scale bar: 2 mm.

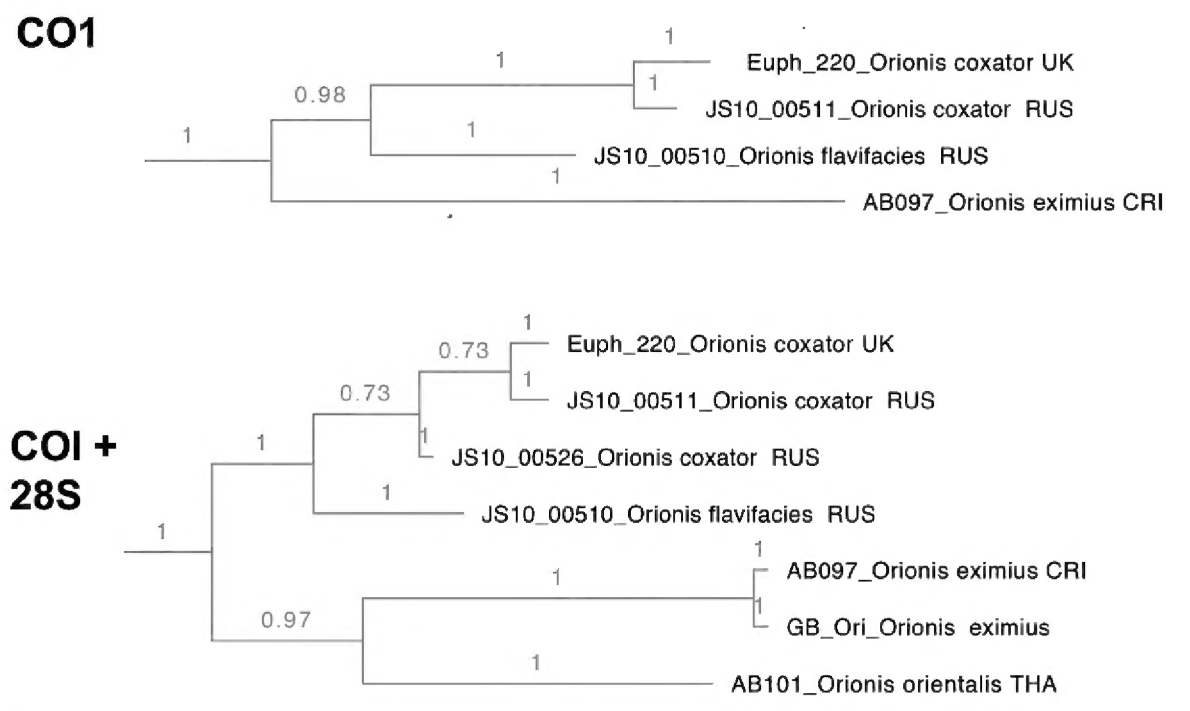

Figure 2. Extract from Bayesian phylogeny of Perilitini: relationships of *Orionis* species based on CO1 and CO1+28S analyses. Numbers on branches are posterior probabilities.

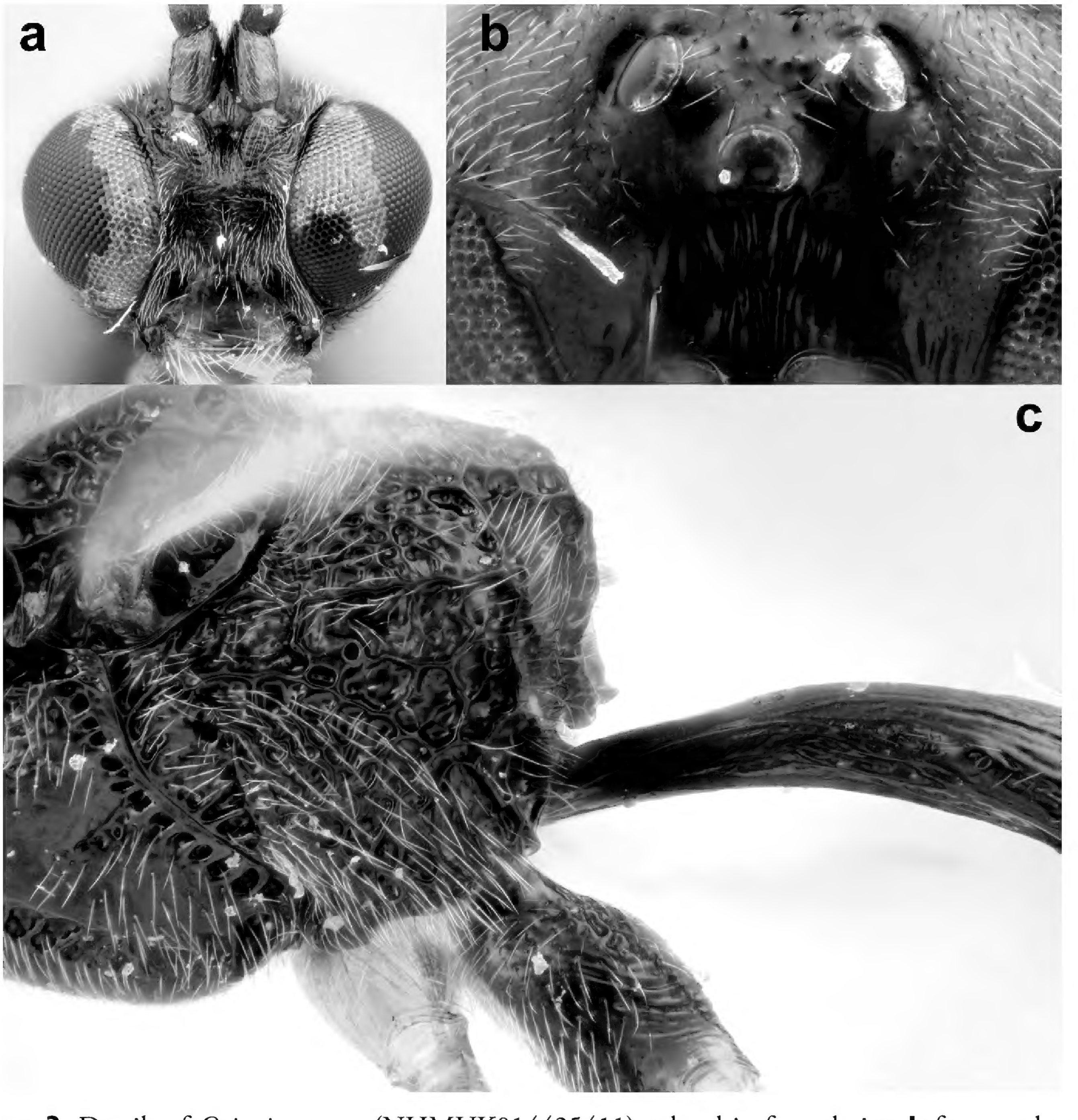

Figure 3. Details of *Orionis coxator* (NHMUK014425411) **a** head in frontal view **b** frons and upper head **c** propodeum, first metasomal segment and hind coxa in dorsolateral view.

(2003) and probably erroneously from the Netherlands by van Achterberg et al. (2020) (see Discussion).

Diagnosis. Mostly black, head with dorsal reddish patches and clypeus reddish brown; scuto-scutellar groove with median carina and several carinulae in pits; propodeum with posterior and dorsal faces angled about 90° relative to each other; hind coxa dorsally rugose-punctate; first metasomal tergite with weak rugae medially.

Orionis flavifacies (Belokobylskij, 2000), new comb.

Perilitus flavifacies Belokobylskij, 2000

Comments. Described from Russia, Primorskiy Territory (Belokobylskij 2000a); recorded from Korea by Papp (2003) based on an identification by Belokobylskij. Russian (Primorskiy Territory) specimen sequenced by Stigenberg et al. (2015).

Diagnosis. Mostly black, head largely yellowish-brown; propodeum with rather rounded division between posterior and dorsal faces; hind coxa dorsally with curved striae; first metasomal tergite largely striate.

Orionis orientalis Shaw & Shimbori, 2016

Comments. Described from Thailand.

Diagnosis. Largely black, head with face and clypeus yellowish-brown, pronotum and propleuron yellowish-brown; propodeum with rather rounded division between posterior and dorsal faces; hind coxa largely unsculptured dorsally; first metasomal tergite largely weakly rugulose.

Discussion

Distribution and ecology of *Orionis coxator*

While this work was in preparation, van Achterberg et al. (2020) reported the occurrence of a very similar specimen in Amsterdam, the Netherlands, which they identified as *Perilitus erratus*. Subsequent posts on Facebook showed that similar specimens have been found in Belgium and Germany recently and a further UK specimen came to light on Facebook (England, Hampshire, New Forest, October 2021; Colin Easton). We strongly suspect that all these specimens belong to the same species and that, as van Achterberg et al. (2020) surmised, this is a recent introduction from the Far East. However, we offer a different perspective on the identification. The Dutch specimen illustrated by van Achterberg et al. (2020) has curved dorsal striae on the hind coxa, identifying this as *Orionis coxator*. Given that two of the authors also described *Perilitus erratus* as a new species (Chen and van Achterberg 1997), perhaps the hind coxa is variable within

the species and these names are synonymous. We have not examined the holotypes of *Perilitus erratus* or *Perilitus coxator* and are relying on the (very informative) original descriptions; should these names prove to be synonymous, *Orionis coxator* has priority.

Whether *Orionis coxator* is native to Europe is probably unknowable, although circumstantial evidence, mainly that these distinctive wasps have never been found in Europe before, strongly suggests that there has been an accidental introduction and perhaps a rapid range expansion within Europe. However, other ichneumonoids have been discovered in Europe following their description in the Russian Far East and these massive range discontinuities have been assumed to represent spot samples from an extensive and undocumented range; for example, the diplazontine ichneumonid, *Episemura diodon* Kasparyan & Manukyan, 1987 (Klopfstein 2014). The distribution of *Orionis* species is rather similar to that of another ichneumonoid genus that was poorly known until recently; *Rodrigama* Gauld, 1991 (Ichneumonidae, Poemeniinae) comprises a few known species, with the type species described from Costa Rica (Gauld 1991) then additional species being discovered in the Oriental and Eastern Palaearctic regions (Matsumoto and Broad 2011; Choi and Lee 2020) and one species in the Western Palaearctic (Broad and Kuslitzky 2019). There are similar examples of apparently huge range discontinuities in Braconidae, for example *Proclithrophorus* Tobias & Belokobylskij, 1981, with the type species (*Proclithrophorus mandibularis* Tobias & Belokobylskij, 1981) described from the southern Russian Far East (Tobias and Belokobylskij 1981) and a second species (*P. genalis* Vikberg & Koponen, 2001), of very similar morphology, subsequently described from Finland (Vikberg & Koponen 2001). Or *Colastes* (*Pseudophanomeris*) *pilosus* Belokobylskij, 1984, known from the Palaearctic Far East, recently being found in Ukraine and the Czech Republic (Belokobylskij 2019). Some parasitoid species suddenly become numerous and then suddenly disappear again. A good example in Britain is *Phrudus badensis* Hilpert, 1987, described from Germany (Hilpert 1987), collected in Britain in good numbers (Shaw 1991) and then apparently disappearing again (M.R. Shaw pers. comm.). *Phrudus badensis* closely resembles *Phrudus longius* Chiu, 1987, described from Taiwan (Chiu and Wong 1987). The lack of known hosts for most of these ichneumonoids hinders interpretation of their distribution.

Orionis eximius is associated with unknown hosts on *Lantana camara* L. (Verbenaceae) (Shaw 1987). *Lantana camara* does not survive outdoors in the cool temperate climate of NW Europe, although other ornamental Verbenaceae do. The as yet unknown hosts of *Orionis* are presumably Coleoptera, as with other Perilitini (Shaw 1985; Stigenberg et al. 2015). The large eyes of *Orionis coxator*, and the fact some specimens have been caught at light (as have some *O. flavifacies*; Belokobylskij 2000a), suggest it is at least partly nocturnal.

Composition of the genus *Orionis*

Orionis is diagnosed by a combination of characters, more than one of which can be present in species classified in *Perilitus*. For example, *Perilitus mylloceri* (Wilkinson, 1929) (originally described in *Dinocampus* Förster, 1863) shares a narrow, ventral-

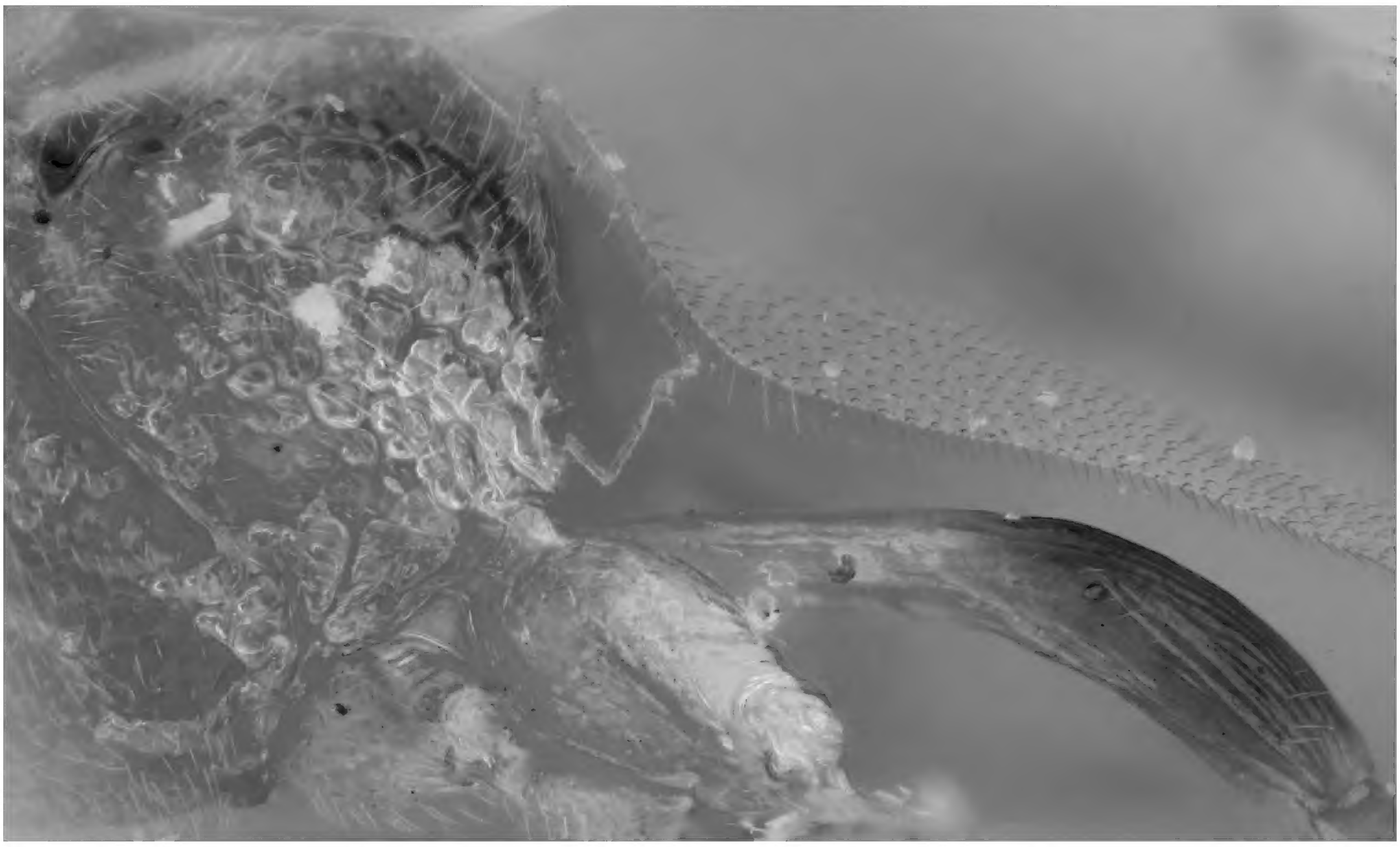

Figure 4. *Perilitus mylloceri* paratype female, propodeum and first metasomal segment.

ly fused first metasomal segment, strongly convex propodeum (Fig. 4) and bulging, ventrally convergent eyes with *Orionis*. However, we consider this species best placed in *Perilitus*, as the spiracles of the first metasomal tergite are at the posterior third and this segment is virtually straight until the postpetiole. An unidentified or undescribed African species of *Perilitus* in NHMUK has a strongly angled propodeum, very similar to some *Orionis*, and ventrally convergent eyes (Fig. 5). In this case, the first metasomal segment is more typical of *Perilitus*, being only 2.5 × as long as posteriorly wide, with the spiracles at the posterior third of the tergite and the sides of the first tergite ventrally distinctly separated. Nevertheless, *Perilitus* as currently defined is probably not monophyletic (Stigenberg et al. 2015; Suppl. material 1, 2) and some of these species might be better classified elsewhere, perhaps in an expanded concept of *Orionis*. Figure 6 compares the propodeum and first metasomal segment of *O. coxator* and *Perilitus rutilus* (Nees, 1811), the type species of *Perilitus*.

Chen and van Achterberg (1997) described *erratus* in the genus *Meteorus*, despite the lack of vein *rs-m* (i.e., the second submarginal cell is open). GRB's first thought was that the English specimen of *O. coxator* could be an aberrant *Meteorus*. The structure of the first metasomal segment and the strongly convergent eyes are both more similar to some *Meteorus* species than they are to *Perilitus*. The first metasomal segment of these Old World species is not as long and slender as in the type species of *Orionis*, *O. eximius* (Muesebeck), which has hindered the correct identification of the Old World species. Bortoni et al. (2016) had recognised *Orionis* as occurring in the Old World, with the description of *O. orientalis* from Thailand, and pointed out the close relationship to certain '*Perilitus*' species in Stigenberg et al.'s (2015) phylogeny. It took a chance discovery of *O. coxator* on a different continent to join the dots and more accurately describe the diversity of *Orionis* species.

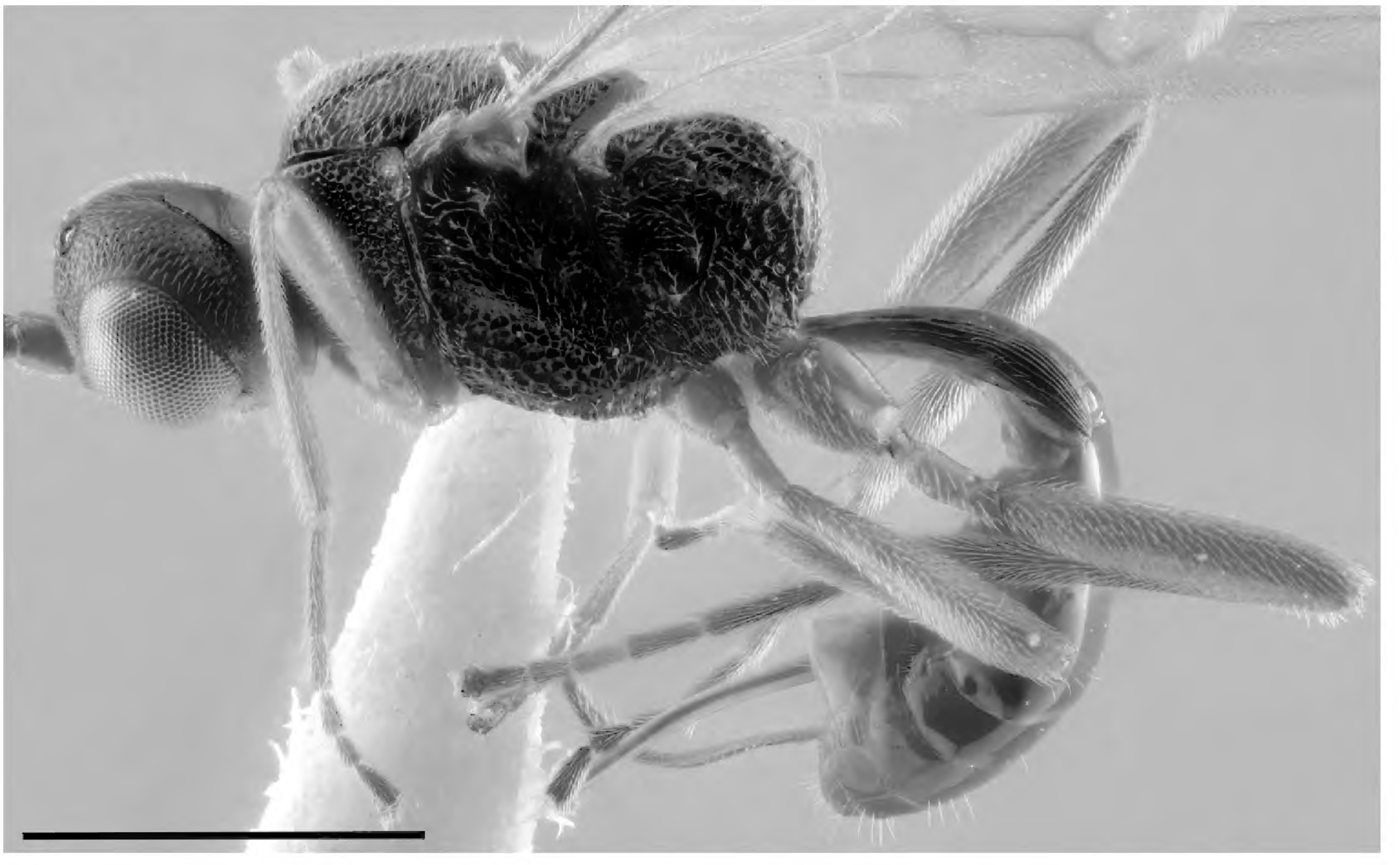

Figure 5. Unidentified *Perilitus* species from Cameroon (NHMUK014425412). Scale bar: 1 mm.

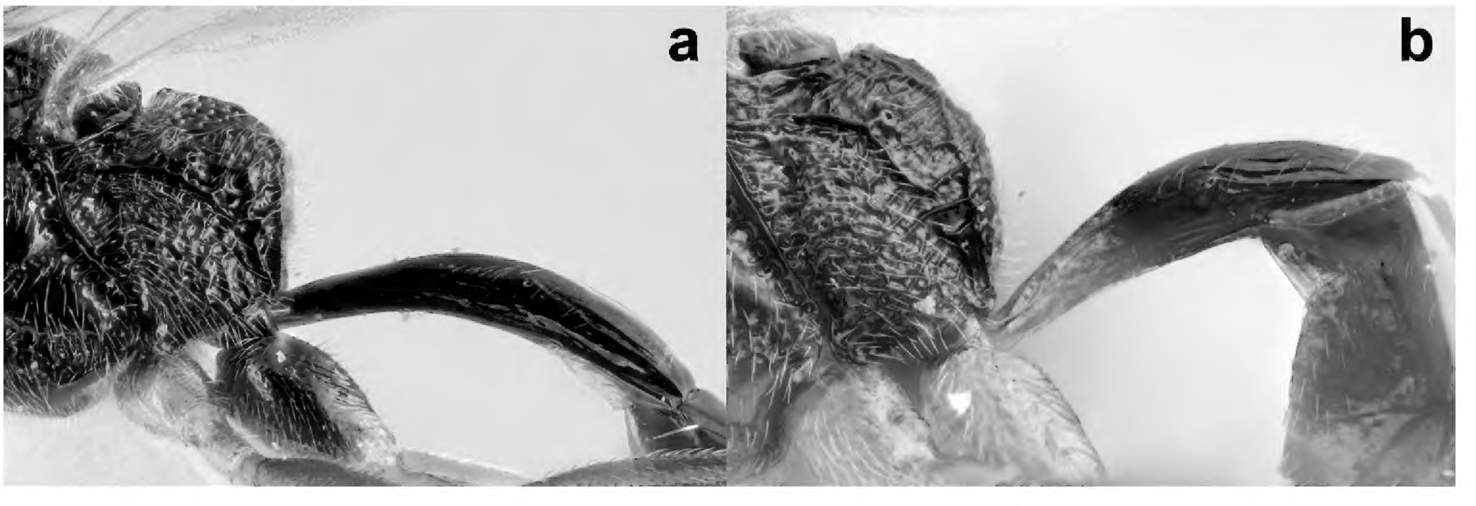

Figure 6. Comparison of propodeum and first metasomal segment of **a** *Orionis coxator* and **b** *Perilitus rutilus*.

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Supplementary material 1

Bayesian analysis of Perilitini based on CO1

Authors: Gavin R. Broad, Julia Stigenberg

Data type: Phylogenetic.

Explanation note: Bayesian analysis of selected Perilitini (Braconidae, Euphorinae) based on CO1 gene.

Link: https://doi.org/10.3897/jhr.88.76177.suppl1

Supplementary material 2

Bayesian analysis of Perilitini based on CO1 and 28S

Authors: Gavin R. Broad, Julia Stigenberg

Data type: Phylogenetic.

Explanation note: Bayesian analysis of selected Perilitini (Braconidae, Eurhorinae) based on combined analysis of CO1 and 28S.

Link: https://doi.org/10.3897/jhr.88.76177.suppl2